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A SMALL NEW ARBOREAL SPECIES OF WEST INDIAN BOA (BOIDAE; *CHILABOTHRUS*) FROM SOUTHERN HISPANIOLA

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ABSTRACT. Thirteen species of West Indian boas (*Chilabothrus*) are distributed across the islands of the Greater Antilles and Lucayan Archipelago. Hispaniola is unique among this group of islands in having more than two species of *Chilabothrus*—three are currently recognized. Here we describe a fourth species from Hispaniola, a newly discovered distinctive species of small boa from the dry forest of the Barahona Peninsula, southwestern Dominican Republic, near the border with Haiti. This new species resembles in body size and in other aspects its closest relative *Chilabothrus fordii* (Günther 1861), with which it appears to be allopatric. The new species, which we describe as *Chilabothrus ampelophis* **sp. nov.**, differs from *C. fordii* in body, head, and snout shape; in scalation; in both coloration and color pattern; and in phylogenetic uniqueness. Some relevant meristic characters from *C. ampelophis* **sp. nov.** fall between *C. fordii* and *C. gracilis* (Fischer 1888), accentuating the morphological and likely ecological differences from its sister species *C. fordii*. The discovery of this new species is especially important as it appears to be among the smallest boid (Boidae) species, has an arboreal specialization, and is found in a very restricted and highly threatened habitat.

RESUMEN. Trece especies de boas de las Indias Occidentales (*Chilabothrus*) se distribuyen a lo largo de las islas de las Antillas Mayores y el archipiélago de las Lucayas. La Hispaniola es única entre este grupo de islas por tener más de dos especies de *Chilabothrus*—tres se reconocen actualmente. Describimos una cuarta especie, una boa pequeña recientemente descubierta, y fácilmente reconocible, del bosque seco de la península de Barahona, en el suroeste de la República Dominicana próximo a la frontera con Haití. Esta nueva especie se asemeja en tamaño corporal y otros aspectos a su pariente más cercano *Chilabothrus fordii* (Günther 1861), de la cual aparentemente es alopatrica. La nueva especie, la cual describimos como *Chilabothrus ampelophis* **sp. nov.**, se diferencia de *C. fordii* en las formas del cuerpo, cabeza y hocico, en escamación, y tanto en coloración de fondo como en el patrón de color. Algunos

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caracteres merísticos relevantes de *C. ampelophis* **sp. nov.** se alojan entre los de *C. fordii* y *C. gracilis* (Fischer 1888), acentuando las diferencias morfológicas y probablemente ecológicas de su pariente más cercano *C. fordii*. El descubrimiento de esta nueva especie es especialmente importante ya que parece ser una de las especies de boas (Boidae) más pequeñas, es de especialización arborícola, y se encuentra en un hábitat muy restringido y amenazado.

KEY WORDS: Caribbean; dwarfism; Dominican Republic; dry forest; phylogenetics; systematics

INTRODUCTION

The Caribbean snake genus *Chilabothrus* currently has 13 recognized species (Reynolds et al., 2013, 2016a,b; Reynolds and Henderson, 2018; Hedges et al., 2019) distributed throughout the Greater Antilles (one species in Cuba, one in Jamaica, three on Hispaniola, and three on the Puerto Rico Bank and Mona Island) and the Lucayan Archipelago (the remaining five species). This genus has been the focus of earlier and recently renewed molecular systematic and phylogenetic studies (Campbell, 1997; Reynolds et al., 2013), including the recognition that *Chilabothrus* is a genus distinct from mainland Central and South American *Epicrates*. *Eunectes* and *Epicrates* are its closest living relatives and all share common ancestors in the late Eocene/early Miocene (Reynolds et al., 2013). In the last 8 years significant taxonomic changes have been made within *Chilabothrus*, with the addition of four species. One of these was a new critically endangered species found in situ (*Chilabothrus argentum* Reynolds et al., 2016a; Reynolds, 2017), whereas three others were elevated from known populations previously considered to be subspecies (Reynolds et al., 2013, 2015; Rodríguez-Robles et al., 2015; Reynolds et al., 2018).

Previous study (Reynolds et al., 2016b) has demonstrated that the genus *Chilabothrus* has radiated to fill a variety of niche spaces on the islands where they occur, most notably in body size. Most islands have a large species, whereas some islands or island groups (e.g., Puerto Rico Bank, Hispaniola, and the Lucayan Archipelago) also have a

small species, occasionally occurring in sympatry with the large species. Small-bodied species have evolved repeatedly in situ on these islands and tend to specialize in restricted niche use (frequently becoming highly or exclusively arboreal; Reynolds et al., 2016b). Hence, it has been suggested that divergence in body size (and associated specialization) has allowed in situ speciation to occur on islands such as Hispaniola, supporting three extant species (Reynolds et al., 2016b). *Chilabothrus striatus* is a large-bodied generalist species, achieving body lengths of > 2 m and occurring nearly islandwide (and on some satellites) to elevations of about 1,200 m (Tolson and Henderson, 1993; Reynolds et al., in press). *Chilabothrus gracilis* is a small and slender arboreal specialist, feeding almost exclusively on *Anolis* lizards and found in relatively mesic lowland regions across Hispaniola (Tolson and Henderson, 1993; Reynolds et al., in press). *Chilabothrus fordii* is another small-bodied species, frequently occurring in arboreal situations at night but also found on the ground underneath cover objects during the day or crossing roads at night in lowland regions that are more xeric (Tolson and Henderson, 1993; Reynolds et al., in press). The topographical complexity of Hispaniola, possessing numerous mountain ranges (including the highest peak in the Caribbean region), coupled with its relatively ancient emergence yields a tremendous heterogeneity of habitats in which species could evolve. It has been 133 years since the last boa (i.e., *C. gracilis*) was described from Hispaniola. Now we describe a new fourth species discovered in situ among xeric



Figure 1. Map of Hispaniola showing the approximate locality of *Chilabothrus ampelophis* (in black) located on the southern slopes of the Sierra de Bahoruco. The range of the sister species *Chilabothrus fordii* (shown in brown) is built from known records as well as predicted habitat on the basis of mean precipitation (from BioClim, rendered in ArcGIS Pro). The localities of two genetic samples of *C. fordii* used in this study are shown as red triangles.

mountainous foothills along the border of Haiti and the Dominican Republic.

METHODS

Field site

While conducting nighttime surveys in a little-studied region of southwestern Dominican Republic, MALT encountered a small and slender boa exhibiting an apparent mixture of characteristics known from other members of the genus, but also exhibiting a unique head shape and body form. This region, composed of karstic limestone of the Barahona Peninsula and the foothills of the southern Sierra de Bahoruco, is an uplifted area above the Río Pedernales, which runs along the Haiti/Dominican Republic border (Fig. 1). The vegetation shifts from relatively mesic along the river to more xeric in the neighboring karst foothills.

Morphological analyses

For the morphological description we follow the terminology and methods of

Henderson (1997) and Reynolds et al. (2016a, 2018). Along with our own data, we use morphometric and meristic data from Sheplan and Schwartz (1974) (Tables 1, 2). We provide percentages (rounded to the nearest 1% except for head length [HL]/snout–vent length [SVL], see below) for body proportions that were shown to be relevant and diagnostic in our specimen series. For those meristic characters exhibiting bilateral symmetry, we give only the highest value of the two sides, excepting supraocular counts, for which the numbers of each side are included. We use size and shape of scales (single plate or shield) in *C. fordii* as a reference for dorsal head-scale counts (supraocular and frontal) in the new specimens. We determined head-scale formula (Sheplan and Schwartz, 1974; Schwartz and Henderson, 1985) by the intersupraoculars (the row of scales between the supraoculars as in Henderson, 1997) or alternatively, the frontal (single plate between supraoculars) and their anterior and posterior adjacent rows.

TABLE 1. MERISTIC CHARACTERS OF *CHILABOTHRUS AMPELOPHIS* SP. NOV. COMPARED WITH *C. FORDII* EXAMINED ($N = 8$), AS WELL AS MERISTICS OF *C. FORDII* PRESENTED IN SHEPLAN AND SCHWARTZ (1974).

Character	<i>C. ampelophis</i>		<i>C. fordii</i> ($n = 8$)		Sheplan and Schwartz (1974)	
	Mean	Range	Mean	Range	Mean	Range
Ventrals	269.5	263–273	250.8	245–256	N/A	231–263*
Subcaudals	89.4	86–93	79.6	76–83	N/A	69–89
Dorsal rows	38.7	38–40	36.1	34–37	N/A	31–39
Supraoculars	—	4/4–8/8	—	1	N/A	N/A
Mode						
Head scale formula	—	3-1-3-4-4-4	—	2-1-2-4-1-3	3-1-3**	2-1-2-4-2-6
Preoculars	2	1–2	1	1	N/A	N/A
Postoculars	5	4–7	5	4–6	N/A	N/A
Loreals	5	4–6	2	1–4	2	1–4
Circumorbitals	16	13–16	10	10–12	10	8–13
Supralabials	15	15	13	12–15	13	11–15
Infralabials	16	15–16	14	12–16	14	12–16
Infraloreals	2	2–4	1	0–2	N/A	N/A

*Only the holotype of subsp. *Chilabothrus f. manototus* reaches to 263 ventrals (Schwartz 1979)

**Only one specimen with divided (2) frontals (intersupraoculars) out of a sample size of 60.

We took measurements using a digital caliper through a dissecting stereoscope and rounded values to the nearest 0.1 mm. We measured SVL and tail length (TAIL) with a string along the dorsum of each specimen, and rounded to the nearest 0.5 mm. Other character abbreviations and descriptions are as follows: HL, from the angle of jaw (posterior to the quadrate) to the center of the tip of the rostral scale; OL (ocular length), horizontal distance across the eye; NO (nostril to ocular), distance from the anterior edge of the eye to the posterior edge of the nares; RO (rostral to ocular), distance from anterior edge of the eye to the center of tip of the rostral; IO (interocular distance),

TABLE 2. MORPHOMETRIC CHARACTERS (MM) OF THE TYPE SERIES OF *CHILABOTHRUS AMPELOPHIS* SP. NOV. AND OUR SAMPLE OF *C. FORDII* ($N = 8$). VALUES IN PARENTHESES ARE MEANS. ABBREVIATIONS ARE EXPLAINED IN THE METHODS SECTION.

Characters	<i>C. ampelophis</i>	<i>C. fordii</i>
SVL	357–697 (560.5)	345–565 (506.6); to 860*
Tail	90–147 (125.2)	80–132 (110.0)
Total length	447–776 (664.8)	425–697 (611.9)
Tail/total length %	18.2–20.1 (19.1)	16.9–18.9 (18.0)
Tail/SVL %	22.2–25.2 (23.6)	20.4–23.4 (22.0)
NW	3.9–6.5 (5.0)	4.6–6.1 (5.3)
HW	7.4–12.8 (9.6)	6.1–9.8 (8.5)
HL	14.3–23.5 (18.2)	14.9–20.1 (17.6)
IO	4.9–7.3 (5.9)	4.9–5.5 (5.2)
OL	2.5–3.5 (3.1)	2.7–3.0 (2.9)
RO	5.1–8.4 (6.4)	5.0–7.2 (6.0)
NO	3.9–6.6 (5.0)	3.8–6.2 (4.8)
IN	2.1–3.3 (2.7)	2.4–3.3 (2.8)

*Maximum SVL in Sheplan and Schwartz (1974) and Tolson and Henderson (1993).

measured across the frontal region at the intersection of the eye with preocular and supraocular scales; IN (internarial distance), narrowest distance between the nares; HW (head width), measured from photographs of living specimens with IO as a scale using ImageJ software and also from preserved *C. gracilis* ($n = 5$); NW (neck width), measured at the level of ventral #2 in *C. fordii*, obtained from three freshly collected specimens. We found a completely intact freshly shed skin in situ, which we collected (MNHNSD 23.3903; Suppl. Fig. S1) and included in our analysis. Its measurements (SVL and TAIL only) and meristics agree with the data on the type series, providing all but labial scale counts. We sexed the individuals in several ways: chiefly using sexual size dimorphism and other morphological features (scalation, proportions, etc.), postcloacal probing in live individuals, by the relative thickness of the base of the tail, and additionally, by the relative length of the pelvic spurs as in Hoefler et al. (2021), although these authors noted that spur-size differentiation is positively correlated with an increase in SVL. We made comparisons with both published data sets (Sheplan and Schwartz 1974) as well as with *C. fordii* and *C. gracilis* specimens we collected (Suppl. Table S1).

Phylogenetic analyses

We obtained tissue samples from a paratype specimen (MNHNSD 23.3900) as well as from two *C. fordii* (from nearer localities; Fig. 1) in the form of dissected muscle tissue stored in 95% ethanol. We extracted whole genomic deoxyribonucleic acid (DNA) using the Wizard SV[®] kit (Promega, Madison, WI). We used the polymerase chain reaction (PCR) to amplify the mitochondrial (mtDNA) locus cytochrome *B* (*CYTB*), which has been shown to be useful in species

identification in boas (Campbell, 1997; Burbrink, 2004; Reynolds et al., 2013, 2016a, 2018). We conducted reactions in a SimpliAmp[®] (Applied Biosystems) thermal cycler and purified and sequenced PCR product in both directions on an automated sequencer (ABI 3730XL) at the Genomic Sciences Laboratory at North Carolina State University (Raleigh, North Carolina). We assembled sequences and verified ambiguous base calls using Geneious 10.2.3 (Biomatters, Auckland, New Zealand). We aligned these four newly generated sequences with *CYTB* sequences from each of the 13 other species of *Chilabothrus* (data from Reynolds et al., 2013, 2016a,b, 2018) using the ClustaLW2 (Larkin et al., 2007) algorithm implemented in Geneious. We estimated a model of nucleotide substitution (HKY + I + G) for the alignment using Bayesian information criterion in jModelTest2 (Guindon and Gascuel, 2003; Darriba et al., 2012).

We inferred a time-calibrated mitochondrial coalescent tree for all species of West Indian *Chilabothrus* using the Bayesian Markov chain Monte Carlo (MCMC) method implemented in Beast v1.10 (Suchard et al., 2018). As in previous studies (Reynolds et al., 2015, 2016b), we estimated a substitution rate for the mtDNA locus from the alignment of West Indian boas by constraining the root node of *Chilabothrus* using a normal prior with a mean of 21.7 Mya and a standard deviation of 1.8 Mya, derived from a fossil-calibrated divergence time analysis of the larger Neotropical boid phylogeny (Reynolds et al., 2013). We ran the MCMC for 100 million generations using a Yule speciation prior and an uncorrelated lognormal relaxed clock model. We repeated the analyses three times with different starting parameter values, sampling every 1,000 generations and discarding the first 1,000 trees as burn-in, to generate effective sample sizes larger than 200 for all parameters. We

assessed convergence of the independent runs by a comparison of likelihood scores and model parameter estimates in TRACER v1.5 (Rambaut et al., 2013). We combined results from the three analyses using Log-combiner v1.8 and generated a maximum clade credibility tree using TreeAnnotator v1.8.

RESULTS

After finding the first specimen of the species herein described, we spent a total of 20 nights surveying the region between August and December of 2020, covering an area of approximately 38 linear kilometers (spatial data from 3 nights unrecorded) during all surveys combined, consisting of a time effort of 1–3 hours and one to three persons for each survey. Elevational range was 40–330 m above sea level (asl). We found a total of five individuals of the new boa plus a shed skin (Figs. 2, 3, S1) within 1 km of airline distance, at elevations between 80 and 105 m. Most surveys yielded no boas, but one night we encountered two individuals. We designated type specimens (more information below) and accessioned them in the collections of the Museo Nacional de Historia Natural Prof. Eugenio de Jesús Marcano (MNHNSD 23.3900–02), the University of Kansas Biodiversity Institute (KUH 352337), and the Museum of Comparative Zoology, Harvard University (MCZ R-197400).

Phylogenetic analyses

We aligned 1,077 base pairs of mtDNA from the *CYTB* locus from the new species (plus two newly sequenced *C. fordii*) with all *Chilabothrus* species. From this alignment we obtained a maximum clade credibility phylogenetic tree from our BEAST analyses containing all species of *Chilabothrus* plus a paratype (MNHNSD 23.3900) of the new

species. We found strong posterior probability (PP) support (> 0.95) across the tree except for two recalcitrant nodes that exist early in the tree subtending some of the early branching among Greater Antillean islands, as well as some well-characterized (e.g., Reynolds et al., 2013) recalcitrant nodes among the Lucayan lineages (Fig. 4). The new boa species is a member of the clade of Hispaniolan boas including *C. fordii* and *C. gracilis*, and is sister to *C. fordii*, sharing a common ancestor approximately 3.76 Mya during the Pliocene (PP = 1, 95% highest posterior density = 5.9–1.7 Mya).

Taxonomy

Chilabothrus ampelophis sp. nov.

Hispaniolan Vineboa

Figures 2, 3, 5–7, S1, S2; Tables 1, 2, S1

ZooBank ID:

urn:lsid:zoobank.org:pub:5FCCB8FE-E24B-4F38-8E02-EC81F2832E55

Holotype. MNHNSD 23.3901 (MALT 00726), a male collected in the hills of Loma La Trinchera, Paso Sena, 4 km N of Pedernales, Pedernales Province, Dominican Republic on 18 November 2020 by M. A. Landestoy and G. Féliz.

Paratypes (four). Same locality as the holotype; MNHNSD 23.3900 (MALT 596), collected 2 August 2020 by M. A. Landestoy, R. Ortíz, and A. Marmolejo; KUH 352337 (MALT 733) on 26 November 2020 by M. A. Landestoy, Y. Corona, and W. Terrero; MNHNSD 23.3902 (MALT 740) and MCZ R-197400 (MALT 741) on 13 December 2020 by M. A. Landestoy and N. Corona.

Diagnosis. A small (maximum SVL = 697 mm) species of *Chilabothrus* (Figs. 2, 3) of slender habitus, with a distinctive neck, a dorsally flattened head and narrow snout, and eyes protruding dorsally above head level and directed anterolaterally. There is a distinctive head scutellation with either



Figure 2. *Chilabothrus ampelophis* sp. nov. Clockwise from top: KUH 352337 (5 December 2020), MNHSD 23.3901 (19 November 2020), MNHSD 23.3901 (19 November 2020).



Figure 3. In situ photos of *Chilabothrus ampelophis* sp. nov. from the type locality. Clockwise from top left: KUH 352337 (27 November 2020), MCZ R-197400 (13 December 2020), holotype specimen MNHSD 23.3901 (19 November 2020).

supraocular, frontal, and parietal (or altogether) scales highly fragmented into numerous small scales (Fig. 5); a moderate to high ventral scale count, a high modal loreal scale count, high modal circumorbital count, and high modal labial counts. The dorsal ground coloration is of dark taupe to tan-brown with a dorsal pattern of dark brown to blackish helix (zigzag) composed of fused narrow diagonal blotches, also with squarish, nearly rectangular or X-shaped blotches running dorsally, with all markings irregularly outlined and bordered with pale cream or whitish cream scales that form highly contrasting stripes or spots. There is a dark brown lateral stripe (at times disrupted) that

branches toward dorsolateral and lateroventral areas, forming a diffuse reticulated effect laterally.

The new species somewhat resembles *C. fordii*, to which it is most closely related (Figs. 5–7) and to which a closer comparison is warranted. *Chilabothrus ampelophis* sp. nov. differs from *C. fordii* (Tables 1, 2) in having a higher number of ventral scales (263–273 vs. 231–263 in *C. fordii*), higher count of subcaudals (86–93 vs. 69–89 in *C. fordii*), and higher count of dorsal scale rows at midbody (38–40 vs. 31–39 in *C. fordii*). Other characters (clearly separable) are: multiple supraoculars (4/4–8/8 vs. a single platelike supraocular in *C. fordii*; Fig. 6), as

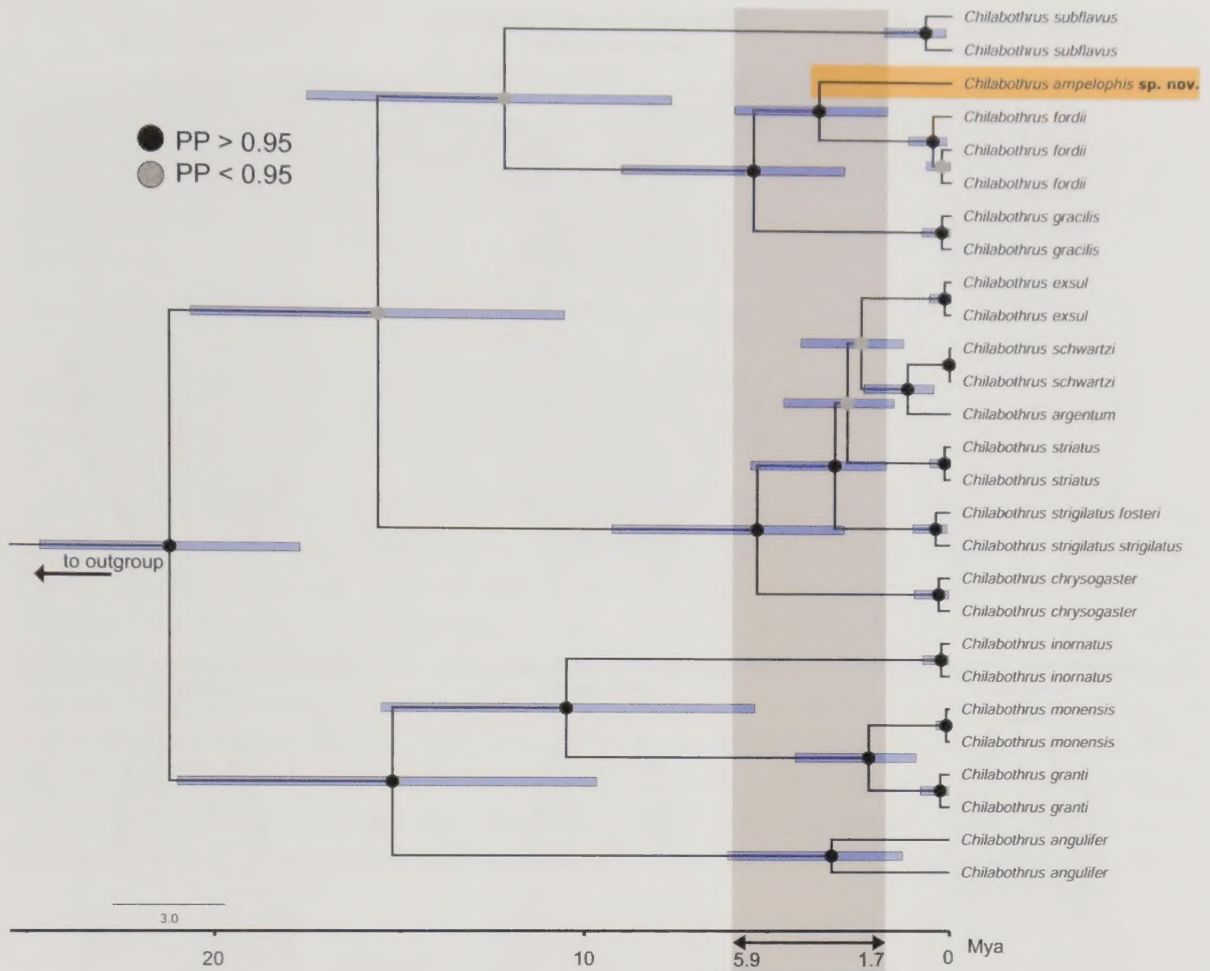


Figure 4. Bayesian ultrametric phylogenetic tree, inferred using BEAST, of the mitochondrial *CYTB* locus generated from all species of West Indian boas. Blue bars represent 95% highest posterior density (HPD) intervals for coalescent time estimates; dark circles represent posterior probabilities (PP) > 0.95; light circles represent PP < 0.95. The scale on the bottom shows coalescent time (Mya), with the gray bar spanning the 95% HPD interval for the estimate of the coalescent time of *Chilabothrus ampelophis* sp. nov. (in orange) and *C. fordii* (5.9–1.7 Mya).

well as multiscale intersupraoculars or short frontal (vs. a single and long, platelike frontal in *C. fordii*) that when single, the frontal covers less than the length of an eye (vs. frontal plate longer than or as long as the eyes in *C. fordii*), with frontal scale variation reflecting on a highly variable head-scale formula (to 4-4-4 in *C. ampelophis*, but modally 3-1-3 in *C. fordii*; Fig. 5). Small, multiple scales are in the first row of prefrontals (vs. large prefrontals basically arranged in three pairs in *C. fordii*), and very

small scales are in the parietal region (vs. larger, at times platelike frontoparietals in *C. fordii*). There are high modal counts in: supralabials 15 (vs. 13 in *C. fordii*), infralabials 16 (vs. 14 in *C. fordii*), loreals 5 (vs. 2 in *C. fordii*), circumorbitals 16 (vs. 10 in *C. fordii*), infraloreals 2–4, mode 2 (vs. 0–2, mode 1 in *C. fordii*), and preoculars 2 (vs. 1 in *C. fordii*).

The new species also differs in having a more distinctive neck (% NW/HW 50–53, \bar{X} = 51 vs. 57–62, \bar{X} = 59 in *C. fordii*), a flatter

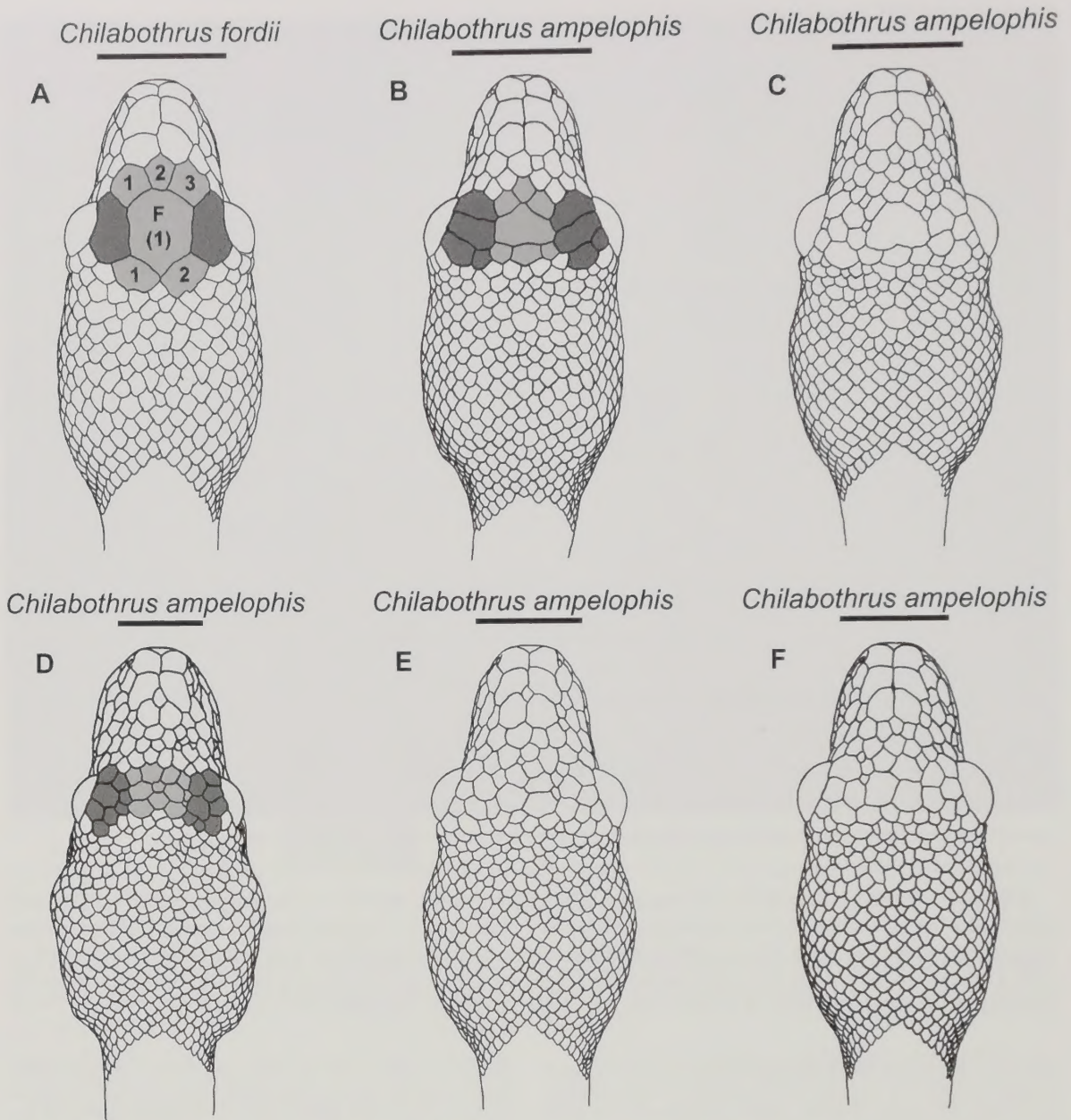


Figure 5. Head shape and scutellation in dorsal view of A, *Chilabothrus fordii* (MNHNSD 23.3904). B–F, type series: MNHNSD 23.3900, KUH 352337, MNHNSD 23.3902, MNHNSD 23.3901, MCZ R-197400, respectively. Head-scale formula is indicated by light shading (intersupraocular or frontal scales) and numbers (3-1-2; F = frontal); dark shading highlights supraocular scales. Scale bars = 5 mm.

head and snout (vs. convex frontal region and a tapered snout in *C. fordii*; Fig. 6), with orbits and supraoculars protruding over the level of the frontal region in profile view (vs. supraoculars below or not protruding over

the frontal region in *C. fordii*; Fig. 6), a more attenuate snout (% IN/IO 42–46, \bar{X} = 45 vs. 49–63, \bar{X} = 53 in *C. fordii*), a slightly longer snout (% RO/HL 35–36, \bar{X} = 35 vs. 31–36, \bar{X} = 34 in *C. fordii*), and a wider interocular

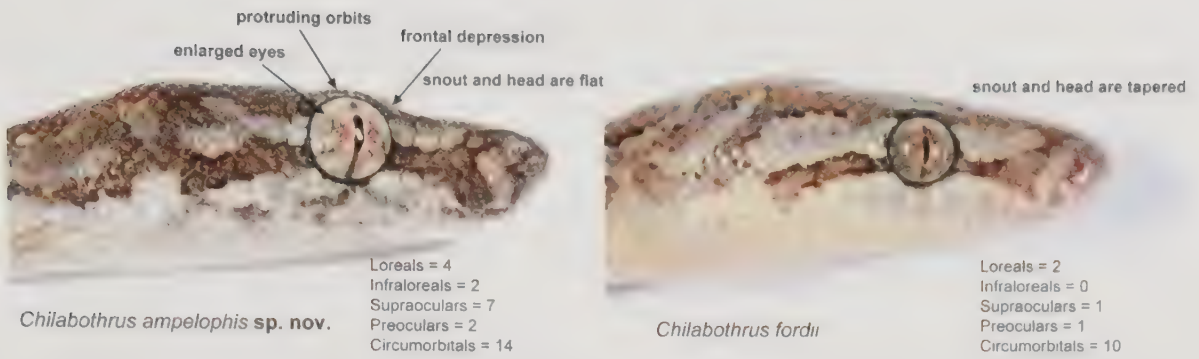


Figure 6. Head and snout profiles of left, *Chilabothrus ampelophis* sp. nov. (MCZ R-197400) and right, *C. fordii* (MNHNSD 23.3906). Note the flat head and protruding eyes and supraoculars above the level of frontal region in *C. ampelophis*; this region is convex with a gradually tapering snout in *C. fordii*.

distance (% of IO, HL 31–35, \bar{X} = 33 vs. 25–33, \bar{X} = 30 in *C. fordii*). *Chilabothrus fordii* has a maximum known SVL of 860 mm (Tolson and Henderson 1993), whereas the largest *C. ampelophis* sp. nov. we observed was 697 mm SVL. Lengths of the TAIL/SVL are moderately higher (22–25, \bar{X} = 24 vs. 20–23, \bar{X} = 22 in *C. fordii*). The dorsal coloration (in life) of *C. ampelophis* sp. nov. differs in having a darker ground color (dark taupe to

tan-brown vs. pale gray to “grayish tan” in *C. fordii*) and in the shape of the primary elements of the dorsal pattern of dark brown to blackish narrow blotches (one to three scales wide at mid-dorsum) diagonally arranged and fused to form a zigzag (Fig. 7); some of the blotches consist of irregularly outlined bold Xs, squares, or rectangles, lined with pale cream scales (vs. pale milk-chocolate brown to medium brown ovate or



Figure 7. Dorsal patterns of A. *Chilabothrus ampelophis* sp. nov. (MNHNSD 23.3901) and B. *C. fordii* (MNHNSD 23.3906). Note the differences in coloration and shape of the primary elements: basically and predominantly a zigzag in *C. ampelophis* and ovate to subcircular blotches in *C. fordii*. Sizes are not to scale.

subcircular blotches three to four scales wide and usually transverse, isolated, and lined with pale gray scales, but see Discussion); venter is pale cream to light gray sprinkled with darker gray and brown (vs. white or dirty white with gray suffusions in *C. fordii*); in preservative, the new species is nearly monochromatic with only ventral pale cream suffusions (vs. brown dorsal pattern and a light beige venter in *C. fordii*); these two species have an allopatric distribution (Fig. 1; see Discussion).

Chilabothrus ampelophis **sp. nov.** differs from another close relative, the also slender and small (maximum SVL to 900 mm) *C. gracilis*, by the orbits and supraoculars protruding above the frontal region (vs. orbits and supraoculars not protruding above the frontal region in *C. gracilis*); also by the longer head (% HL/SVL 3.0–4.0, \bar{X} = 3.4 vs. 2.4–2.7, \bar{X} = 2.5 in *C. gracilis*), longer snout (% NO/HL 27–28, \bar{X} = 27 vs. 23–25, \bar{X} = 24 in *C. gracilis*), much more attenuated snout (% IN/HL 14–15, \bar{X} = 15, IN/HW 26–29, \bar{X} = 28, and IN/IO 42–46, \bar{X} = 45 vs. 18–21, \bar{X} = 19, 31–36, \bar{X} = 33, and 49–55, \bar{X} = 53, respectively), narrower neck (% NW/HW 50–53, \bar{X} = 51 vs. 38–51, \bar{X} = 44 in *C. gracilis*), and smaller eye (% OL/HL 15–18, \bar{X} = 17 vs. 18–21, \bar{X} = 20). There are also multiscale intersupraoculars or short frontal (vs. a single and long platelike frontal in *C. gracilis*), a lower count of ventrals (263–273 vs. 271–304 in *C. gracilis*), and lower count of subcaudals (86–93 vs. 90–111 in *C. gracilis*). It is further differentiated by the shape of the primary elements of dorsal pattern (dark brown to black zigzag, X-shaped, squarish, and rectangular blotches vs. ovate to subcircular dark brown body blotches); their distributions are allopatric (see Discussion).

From sympatric *C. striatus*, *C. ampelophis* **sp. nov.** differs in having a diminutive body size (maximum known SVL 697 mm vs.

maximum SVL > 1,900 mm; Reynolds et al., 2016b), orbits and supraoculars protruding above the frontal region (vs. orbits and supraoculars not protruding above the frontal region in *C. striatus*), fewer ventrals (263–273 vs. 266–299 in *C. striatus*), fewer dorsal scale rows at midbody (38–40, modally 38 vs. 35–65, modally 48 or more in *C. striatus*), infralabials modally 16 (vs. 18 or 19 in *C. striatus*), loreals modally 5 (vs. 1 or 2 in *C. striatus*). The shape of the primary elements of the dorsal pattern also differs (dark brown to black zigzag, and X-shaped, squarish, or rectangular blotches vs. 60–122 stripes or elongated blotches, often virtually patternless in *C. striatus*).

Description of the Holotype. Size small (SVL = 629 mm); weight (in life) 35.4 g; habitus slender (body somewhat laterally compressed); TAIL/SVL 23%; head distinct from neck (NW/HW 53%), flat in profile view; snout attenuated (IN/IO 42%), rather long (RO/HL 36%), flat, and straight with subacuminate tip in profile; eyes large (OL/HL 17%), protrusive, and directed anterolaterally, protuberant to the frontal level (profile view; Fig. 6); ventral scale count moderate to high (273; Table 1), subcaudals moderate to high (88), dorsal scale rows at midbody 40, with a head-scale formula of 4-2-4, supraoculars 8/8, supralabials 15, infralabials 16, loreals 5, circumorbitals 13, preoculars 1, infraloreals 2, with three supralabials in contact with the eye (7, 8, and 9 on the right side, and only two, 8 and 9, on the left side).

Coloration and Pattern in Life of the Holotype. Dorsal ground color tan-brown grading into taupe to pale gray on the sides, with scales stippled with dark brown. The dorsal primary elements form a series of very dark (dark brown to black) narrow diagonal blotches that are mostly fused, creating a zigzag effect, but also some isolated irregular X-shaped, squarish, and rectangular blotch-

es are present, all bordered with whitish-cream scales (Fig. 7); two paramedian longitudinal dark-brown to blackish stripes on the neck departing from the occiput to ~11 scales back, each of a width of three to four scales, edged by a thin (one-scale wide) nearly continuous pale cream line. A lateral dark-brown stripe that originates at the head (evident to midbody but reappears posteriorly) and repeatedly and irregularly branches toward dorsolateral and lateroventral areas, forming somewhat diffuse reticulated markings. Venter pale cream to taupe patterned with brown to dark-brown stippling and freckling, and peripheral smudges on ventral scales that gradually increase in occurrence and density posteriorly; subcaudals mostly dark brown (from subcaudal 13 to tip of tail) especially at the center.

Head Pattern. The basic head pattern is consistent in the series. Dorsal surface of head: dark brown overall with taupe suffusions on the interorbital and prefrontal areas, having the center of the parietal area with a faint pale cream bilobed figure bisected posteriorly, followed by six diffuse pale cream spots arranged transversely with two anteriorly and four posteriorly in the occipital region, each encircled by dark-brown to blackish scales, and pale cream lobes entering sides of parietal areas from the temporal region (from postocular pale Y-shaped stripe, see below).

Lateral head pattern: two horizontal Y-shaped stripes, one of which is a postocular pale cream stripe and the other is a preocular dark brown stripe. The former is rather asymmetrical, with upper lobe shorter, extending briefly to the dorsal surface of the head, bordered below by a dark brown stripe that descends posteriorly (and connected but not aligned to the lateral body stripe) to the base of the posteriormost supralabial scale. It reappears as a preocular Y-shaped dark brown stripe bisected (disrupted on the right

side only in the holotype; Fig. 6, MCZ R-197400 illustrated) by a pale nasal area extending to the adjacent (second) supralabial delimited by the dark first supralabial; a preocular-canthal pale cream stripe enters the upper loreal area and a dark brown stripe below the eye (at the eye-contacting infralabials 7–9, barely continuing to 10), followed by pale areas of labials; the rostral scale is whitish cream at its center.

Infralabials whitish, six anteriormost tipped (on the mouth edge) with very dark brown spots, and irregular stippling and dark brown freckling at posterior infralabials. Chin and throat whitish cream, with dark-brown stippling concentrated at the mental scale and first two infralabials, and at the outer edges of the throat, especially to the posterior infralabials and at the intersection with gulars.

Coloration and Pattern in Preservative. Pattern as described in life but coloration nearly monochromatic with only ventral pale-cream suffusions.

Variation. The only known female (MNHNSD 23.3902) is the largest specimen (SVL 697 mm) in the series and has the lowest ventral (263) count. It has a stubby tail; thus no full subcaudal count or tail proportion could be obtained. In general appearance, this specimen is less slender than the rest in the series, as it has a less compressed body habitus and a more prominent posterior portion of the head (occipital bulge; Suppl. Fig. S2). In body proportions, it has the longest snout (NO/HL 28% and RO/HL 36%), the smallest eyes (OL/HL of 15% vs. 17–18% in other specimens), shortest interorbital distance (IO/HL 31% vs. 32–35%) and an attenuated snout (IN/HW 26% vs. 28–29%), the highest number of supraocular scales (8/8), the highest head formula (4-4-4), and the highest number of loreals (6). The coloration both in life and in preservative of this specimen is much darker

than in the other specimens, and a less accentuated countershading (dorsoventral contrast) is remarkable. Some of the very pale dorsal whitish-cream scales are enveloped within the dark-brown to black blotches (Suppl. Fig. S2). The general coloration of this specimen in preservative is monochromatic.

MNHNSD 23.3900, the smallest specimen (SVL = 357), has the fewest supraocular scales (4/4), the widest interorbital distance (IO/HL 35% vs. 31–33%, IO/HW 64% vs. 57–63%), and the most attenuated snout (IN/IO 42% vs. 45–46%). It has a more contrasting (countershading) coloration of the brown dorsal ground color with more solid-black elements (and their pale outlines) of the dorsal pattern against a pale-cream venter. In preservative, its venter appears light beige in comparison with others in the type series in which the venter is duller or darker.

Natural History. One *C. ampelophis* **sp. nov.** (357 mm SVL) was found stretched out horizontally at 1.5 m on a thin branch of the legume *Senna atomaria* beside a narrow logging trail on the slope of a hill at Loma La Trinchera. If the snake was actively foraging or in a sit-and-wait posture to ambush prey is unknown. A boa (629 mm SVL) was encountered at 2340 h stretched out at 3.0 m in a *Phyllostylon rhamnoides* tree. One individual (486 mm SVL) was found at 2240 h, coiled and apparently inactive at 1.25 m in a young *Acacia skleroxyla* tree. The tree was surrounded and overlapped by vines, under cover of ~70% of the main canopy of an 8-m-tall *P. rhamnoides*. At 2000 h, another boa (697 mm SVL) was spotted stretched out and moving slowly at 3.5 m in a ~6.0-m-tall *Bursera simaruba* tree. Another *C. ampelophis* **sp. nov.** (564 mm SVL) was found at 1930 h stretched out at 2.0 m and moving slowly from a *P. rhamnoides* to a cactus.

All five individuals of *C. ampelophis* **sp. nov.** were encountered at night and four of the five were active (one was coiled and inactive). On the basis of limited data, *C. ampelophis* **sp. nov.** is likely an active forager that hunts for quiescent prey, primarily *Anolis* lizards, at night. Lizards in general and anoles in particular are abundant and ubiquitous and are important components in the diets of many West Indian snakes, including boids (Henderson, 2015; Reynolds et al., in press). The foraging behavior and diet of *C. ampelophis* **sp. nov.** likely parallels that of the similarly slender and highly arboreal *C. gracilis*.

While being photographed, the tails and parts of the posterior portions of the bodies of two of the boas (MNHNSD 23.3901—the holotype—and KUH 352337) became rigidly straight while the posterior portion of the snakes' body was hanging off a branch or even while the snakes moved and slid away in a stealthy manner. We suggest this behavior may have the purpose of balancing or crypsis (i.e., simulating a smaller branch from the one supporting most of the boa's body). MNHNSD 23.3902 and MCZ R-197400 whipped and undulated the tail when grabbed anteriorly, possibly in an attempt to distract attention away from the head. When touched on the head MNHNSD 23.3902 flattened its snout and widely gaped its mouth. Also, when handled, most individuals coiled into a tight ball with the head hidden. Voiding of the cloaca and musking were also used as defense strategies. Only one of the boas attempted to bite, and it was in a preshed condition.

Although no predation has been observed, we suspect that predators of *C. ampelophis* **sp. nov.** are likely the same as those that prey on *C. fordii* and *C. gracilis* (e.g., raptors, cats, rats).

Etymology. The epithet is from ancient greek *ampelos*, meaning vine, in allusion to

the slender body and head shape, which is rather unusual for the genus, and for the relative abundance of vines in the dry rocky habitat at the type locality. The suffix *-ophis* refers to a snake, hence the epithet is translated as “vinesnake.”

Suggested Common Name. Hispaniolan Vineboa

DISCUSSION

Reynolds et al. (2016b) found that small body size is an adaptation to substrate specialization and that an overlooked species like the one described herein being both small bodied and an arboreal habitat specialist is not surprising. Snake species with which it shares its habitat include *C. striatus*, *Tropidophis* sp., *Hypshyrinchus ferox*, *Uromacer frenatus*, and *Uromacer oxyrhynchus*. The only other boa occurring sympatrically with *C. ampelophis* sp. nov. in this region of Hispaniola is the large generalist *C. striatus*. The new species may fill a niche similar to that of the related but allopatric *C. fordii* or *C. gracilis*, and assuming an allopatric scenario of speciation of a shared ancestor with *C. fordii* is parsimonious. A population of *C. gracilis*, a species with somewhat similar body proportions to *C. ampelophis* sp. nov., is known from near the Barahona Peninsula approximately 60 km northeast (Los Patos, Barahona), but the coast northeast of the peninsula is much more mesic, representing a barrier for dry-forest species (see below). Schwartz (1980) commented on a northern (north “paleo-island”) origin of *C. fordii* on Hispaniola and suggested that the species invaded the south (south “paleo-island”), reaching as far south as the lower northern slopes of the Sierra de Bahoruco. This mountain chain, which extends from the coast southeast of the Valle de Neiba west into the Tiburon Peninsula in Haiti as the Massif de la Selle, rises as high as ca.

2,700 m asl (ca. 2,400 m on the Dominican side; de la Fuente, 1976). A gradient of habitats includes broadleaf, cloud, and pine forests toward the summit, and these habitats and elevations are likely barriers for dispersal of lowland, especially xeric-adapted, species. Similarly, the mesic eastern portion of the Sierra de Bahoruco abruptly descends and meets the coast of the northeastern section of the Barahona Peninsula, isolating some xeric lowland species north to south, and vice versa (Schwartz’s so-called “Barahona Entrapment”), although certain species managed to circumvent this barrier (Schwartz 1980).

Substrate specialization, such as arboreality, appears to evolve in tandem with relative body proportions in snakes (Lillywhite and Henderson, 1993; Pizzatto et al., 2007; Feldman and Meiri, 2013; Reynolds et al., 2016b) such that arboreal snakes tend to be slender and lightweight, with longer prehensile tails and different axial skeletal musculature (Jayne, 1982; Lillywhite and Henderson, 1993; Sheehy et al., 2016 and references therein). In *Chilabothrus*, arboreal specialists are not only smaller bodied than substrate generalists, but they also tend to have elongate and slender bodies. *Chilabothrus gracilis* was previously considered the most slender and specialized boid snake (Henderson and Powell, 2002), but *C. ampelophis* appears to be smaller and just as slender. Arboreal West Indian boas (*Chilabothrus* spp. and *Corallus* spp.) forage nocturnally along terminal branches, shrubs, and grasses for sleeping *Anolis* lizards, and hence substrate structure might impose the strongest selective constraints on body shape and size in *Chilabothrus* (Chandler and Tolson, 1990; Rodríguez-Robles and Greene, 1996; Reynolds et al., 2016b). Further, small body size and associated substrate specialization have evolved repeatedly in the genus *Chilabothrus* since the

Miocene (Reynolds et al., 2016b). Thus, apparently *C. ampelophis* sp. nov. is yet another example of island in situ speciation yielding specialist boas on the same island, albeit adapted to different habitats (*gracilis*, arboreal mesic forests; *fordii*, xeric forests and scrubland; *ampelophis* sp. nov., mesic to xeric dry/seasonal forest), presenting additional evidence of deterministic evolution in the genus.

Besides the structural and proportional differences in *C. ampelophis*, the head scutellation seems unique among small Hispaniolan *Chilabothrus*. In addition to specimens we have examined, other works illustrate the single-plate (or shields) head scales, especially the frontal and supraoculars (Fischer, 1888; Cochran, 1941; Walls, 1998). Of interest, Tolson (1987) noted that head shields are highly fragmented in embryos and neonates in some of the species, and at least in the related *C. fordii*. That author observed that such fragmentation increases the number of intersupraocular (frontal) scales, which decreases as the SVL increases in specimens, hence indicating an ontogenetic shift in head-scale size and number. Specimens of *C. fordii* of comparable or even smaller sizes than *C. ampelophis* appear to maintain integrity in the head shield's size and number.

In their description of the dorsal pattern of *C. fordii*, Sheplan and Schwartz (1974) commented that most specimens have the ovate or subcircular blotches fused to form a chainlike effect. Although we did not examine their series and no illustrations of that pattern were shown, we assume that it is the feature that most resembles the arrangement of the dorsal primary elements in the *C. ampelophis* sp. nov. zigzag effect; thus, in Fig. 7 we compare the available *C. fordii* specimen that best matches that description in Sheplan and Schwartz (1974). Whichever the case, the blotches in *C. ampelophis* sp. nov.

are much narrower than those in *C. fordii*, and this pattern is constant in all specimens, in contrast with that in *C. fordii* in which the areas where blotches fuse to produce the chainlike effect are localized or more restricted (Sheplan and Schwartz 1974). Those authors also added that "in other individuals, some of the dorsal blotches are inverted Ys." As already noted, other elements found in the dorsal pattern of *C. ampelophis* sp. nov. are X-shaped, squarish, or nearly rectangular blotches. Images depicting the dorsal pattern of *C. fordii* (Fischer, 1888; Tolson, 1987; Tolson and Henderson, 1993; Walls, 1998; Henderson and Powell, 2004) are consistent with our material. Besides the more frequent occurrence of the zigzag in *C. ampelophis* sp. nov., its disposition and both the coloration itself and that surrounding it (Fig. 7) make it clearly distinct from the dorsal pattern of *C. fordii*.

Other features such as neck breadth (NW/HW) and large eye size (OL/HW) are evident in the new species, but at least one of the relevant characters with which to calculate ratios or proportions (HW) seems unreliable when measured from older specimens of other species for comparative purposes, since it might be affected by artifacts of preservation (e.g., squeezing or shrinking of the head laterally). Considering the available small sample size, we also used HL as a value to calculate by the OL (see Methods). These body conditions are noteworthy as Hedges and Garrido (1992) and Hedges (2002) suggested that they are correlated with arboreality in Cuban snakes of the genus *Tropidophis*. These values could be easily and perhaps more reliably obtained from live individuals of this species and others for comparison without having to collect them. The finding of additional individuals of *C. ampelophis* sp. nov. would allow us to determine if the apparent intraspecific morphological differentiation (head scalation,



Figure 8. Habitat of *Chilabothrus ampelophis* sp. nov. in the southwestern corner of the Dominican Republic. A, aerial drone photo from March 2021 showing general habitat consisting of forested rolling hills from 200- to 400-m elevation where all specimens of *C. ampelophis* sp. nov. were found. B and C, photos showing habitat characteristics of the type locality for *C. ampelophis* sp. nov. D, agricultural encroachment along the foothills of the type locality.

ventral counts, body habitus, and eye and snout proportions) is indeed owing to sexual dimorphism or to allometric patterns.

As noted by Mahler et al. (2016), the age of discovery of remarkably distinct new species of vertebrates is not over, even in fairly well-known (although highly diverse) regions of the Caribbean, as recent work has demonstrated (Turvey et al., 2015; Reynolds et al., 2016a; Landestoy et al., 2018; Rodríguez-Silva et al., 2020). Nevertheless, the last boa to be described from an in situ discovery in the Greater Antilles (*Chilabothrus subflavus* Stejneger) was 120 years ago. *Chilabothrus ampelophis* sp. nov., likely is among the smallest members in the genus and in the family Boidae and is another notable example of ecological diversification

on an island of extensive geological complexity.

Conservation concerns

The type locality of *C. ampelophis* sp. nov. lies along the Dominico-Haitian border and remains quite well forested, at least along the road edges of the foothills, although intensive agriculture in the neighboring lowlands and wood charcoal production is happening directly at the type locality (Fig. 8). Also, habitat alteration in the form of removal of the small trees and bushes of *Amyris* spp., the essence of which is eventually exported overseas for the perfume industry, is occurring locally. The destination of all these forest products is the neighboring country of Haiti. Also, free-roaming cattle may negatively affect the habitat. Other threatened

species (*Peltophryne armata*, *Anolis strahmi*, *Sphaerodactylus plummeri*, *Sphaerodactylus thompsoni*, an undescribed *Tropidophis*, and *Mitophis pyrites*) are found here. We anticipate that the habitat of this new species is under threat from these resource exploitation activities, and we urge additional work to further characterize the conservation status of the species.

We suggest that *C. ampelophis* **sp. nov.** satisfies International Union for the Conservation of Nature Red List criteria for a listing of Critically Endangered. The species is known from a single locality of $\ll 10$ km² that is actively experiencing reduction in habitat quality owing to charcoal production, selective vegetation harvest, and clear-cutting for agriculture (Criteria B2a,b). Ecologically similar areas to the south and east of the type locality have been extensively studied by herpetologists for decades, without having sighted this new species. We believe that it is highly localized near the type locality. We anticipate that further research on the species will reveal that it satisfies additional criteria for Critically Endangered as well.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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